

RECONSTRUCTION OF CRANIAL MORPHOLOGY AND ANALYSIS OF FUNCTION IN THE PLEISTOCENE GROUND SLOTH *NOTHROTHERIOPS SHASTENSE* (MAMMALIA, MEGATHERIIDAE)

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ABSTRACT. The masticatory muscle structure of *Nothrotheriops shastense* was reconstructed by examination of scars of muscle origin and insertion. Structural details and function of masseter-ptyergoid and temporalis muscles were reconstructed based upon comparisons with the tree sloths *Bradypus* and *Choloepus*. Dental studies show that *Nothrotheriops* had an anteromedially directed masticatory power stroke as do tree sloths and most other therian mammals studied to date. The shape and orientation of the ascending and descending zygomatic arch processes in *Nothrotheriops* can be explained in biomechanical terms to emphasize the mechanical advantage of the masseter complex muscles. Restoration of other cranial soft tissues demonstrates a nasal region in *Nothrotheriops* longer than has been shown previously; therefore a new longer face (a primitive condition among sloths) is proposed for this genus. In general, *Nothrotheriops* appears to be closer in cranial structure to *Bradypus* than *Choloepus*, although *Nothrotheriops* lacks an extremely short face (a derived condition unique to *Bradypus*). These and other derived structural similarities, such as the absence of elongate caniniform teeth, an elevated craniomandibular joint, elongated pterygoid flanges, and unusually oriented lateral pterygoid muscles, support the derivation of *Bradypus* from the megatheriid ground sloth lineage with *Nothrotheriops*, and also the structural but not functional distinction from *Choloepus*, which is probably more closely related to the megalonychid ground sloth lineage.

INTRODUCTION

The genus *Nothrotheriops* from the Pleistocene of North America, belongs to the Megatheriidae, one of three extinct ground sloth families recognized by Simpson (1945). These families are distinct morphologically, and differ greatly (especially in locomotor habits) from Recent tree sloths. Sloths are herbivorous, feeding primarily upon leaves (Montgomery and Sunquist, 1978), although some species may have ingested grasses and fruits. Martin et al. (1961) and Hansen (1978) have shown that the diet of *Nothrotheriops* was varied,

including 72 genera of herbaceous and woody plants as well as grasses.

CRANIAL ANATOMICAL TRENDS IN PILOSANS

Before considering functional patterns in sloth cranial muscles it is important to review the xenarthran structural inheritance. Several authors (Hirschfeld, 1976; Hirschfeld and Webb, 1968; Winge, 1941; Patterson and Pascual, 1972; Webb, 1985) suggest that early xenarthrans were primarily insectivorous, and that specializations for insectivory restricted later herbivorous members of the group from developing a typical herbivore feeding apparatus.

The earliest known (Oligocene) sloths were herbivores, although they retained influences derived from insectivorous or myrmecophagous xenarthrans. Some of the important characters were: (1) greatly elongated skulls, particularly in the nasal region; (2) a reduced zygomatic arch, including loss of the anterior-posterior connection; (3) reduction of the importance of mastication; (4) loss of tooth enamel; (5) simplification of tooth shape; (6) reduction in tooth number with the loss more complete anteriorly; and (7) a rather small buccal opening to prevent accidental loss of live prey by insectivorous animals.

Tongue elongation in all living xenarthran groups (Naples, 1985b; Reeve, 1939; Owen, 1854; Macalister, 1875; Montgomery, 1985) and its precise control by large tongue and hyoid muscles, as in Recent tree sloths (Naples, 1986) enabled early insectivorous xenarthrans to ingest many rapidly moving aggressive insects in as short a period of time as possible (Montgomery, 1985). The ability to protrude the

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tongue far from the mouth enhanced prey capture in insectivorous xenarthrans (Montgomery, 1985). Tongue elongation was accommodated by nasal elongation, which became extreme in the xenarthran anteater lineage, culminating in *Myrmecophaga*, the largest xenarthran anteater, with a nasal region twice as long as the skull posterior to the eye (Reeve, 1939). The narrow anterior nasal region provides an excellent channel through which the tongue can be aimed precisely. Observations show that anteaters swallow their prey whole (Montgomery, pers. commun.) and rhythmic contractions of the lateral walls of the elongate buccal region convey insects toward the pharynx (Naples, 1985b). Although extreme development of these characters was unlikely in sloths' antecedents, their degree of specialization was influential in limiting facial adaptability when the protosloth lineage acquired tendencies toward herbivory.

Many anatomic trends shown by insectivorous xenarthrans were modified or reversed in animals that became herbivorous. For adequate digestion, leafy material must be cut into pieces fine enough to increase surface area sufficiently for enzymatic breakdown. Additionally, food must remain in the intestinal tract long enough for the nutrients to be absorbed. Leaves require more initial mechanical breakdown than insects, and therefore herbivorous xenarthrans need to chew rather than merely to swallow food, and to retain it longer for digestive processing. Recent tree sloths defecate approximately once per week, and thus retain foodstuffs for a long time in the intestinal tract (Beebe, 1926; Britton, 1941; Goffart, 1971; Montgomery and Sunquist, 1975).

Xenarthrans lost enamel covering the teeth early in their history, but many fossil and Recent armadillos as well as ground and tree sloths have hard dentine surrounding the softer central dentine in their teeth. The differential dentine hardness allows formation of more resistant cutting edges separated by basins. Although most sloth genera retain simple-shaped teeth, they become larger in some lineages. In sloths all teeth are open-rooted, and some forms have continually sharpened caniniform teeth.

In the herbivorous pilosan lineage the typical small myrmecophagous or partially myrmecophagous buccal opening was enlarged for ingesting bulky leafy foods. Concurrently, the change toward herbivory reduced the importance of an extremely elongate tongue. However, the sloth lineage did retain large tongues important to tree sloths in food acquisition. X-ray cinematography and observation by the author reveal that sloths also manipulate foods extensively inside the mouth and against the mandibular premental spout with the tongue. Sloths have large, ossified, fused hyoid bones, moved by large, specialized muscles (Naples, 1986). In comparison with Recent anteaters, sloth masticatory muscles are larger and specialized to provide stronger bite forces at the teeth within the confines of the pilosan structural inheritance.

A RATIONALE FOR MUSCLE RECONSTRUCTION

Postulation of feeding mechanisms in *Nothrotheriops* requires cranial muscle reconstruction. Barghusen (1973) sug-

gested that muscle reconstructions depend upon knowledge of muscle differentiation, distribution, and attachment patterns in living animals. Therefore the significance of cranial muscle scars in *Nothrotheriops* was determined from comparison with Recent tree sloths. Crania of both genera of Recent sloth were dissected (Sicher, 1944), and the internal architecture of the masticatory muscles determined (Naples, 1985a, 1986). Although the relationship between Recent and fossil sloths remains unclear, similarities in cranial structure between these groups serve as a basis for interpreting fossil sloth morphology. Structurally, *Nothrotheriops* crania resemble the Recent tree sloth genus *Bradypus*; both show similarities in general skull shape and lack caniniform teeth. The masticatory muscles left extensive scars of origin and insertion upon sloth crania, allowing detailed muscular reconstruction. Other muscles were less easily interpreted because muscle scars were uninformative, nonexistent (superficial facial muscles), or the bony elements were unavailable for study (tongue and hyoid muscles). Therefore few superficial facial or tongue and hyoid muscles will be considered.

A preliminary report on the masticatory musculature in *Nothrotheriops shastense* was presented at the annual meeting of the Society of Vertebrate Paleontology, 1978, in Toronto, Ontario. Further studies of these fossils were subsequently postponed until completion of comparative structural and functional studies of the crania in Recent tree sloths (Naples, 1982, 1985a, 1985b, 1986).

MATERIALS AND METHODS

Nothrotheriops specimens examined in this study were recovered from the Rancho La Brea tar deposits and housed in the Page Museum of La Brea Discoveries, Los Angeles. One additional well-preserved specimen on display at the Yale Peabody Museum of Natural History, New Haven, was studied (Table 1). Muscle terminology agrees with other studies of Recent tree sloths (Naples, 1982, 1985a, 1985b, 1986), and names of muscles and their parts have been homologized with those in the older literature. Muscle and muscle segment identifications in Recent sloths were determined by tracing innervations in several specimens. For muscular reconstruction in the fossils the same innervations have been assumed, although the paths cannot be traced. Muscles reconstructed in *Nothrotheriops* are listed (Table 2) according to the arrangement of muscle groups based upon common or homologous innervation in the Recent tree sloths.

In predicting the distance to which *Nothrotheriops* could gape, the degree of muscle fiber stretch was estimated. Although actual muscle fibers were unavailable, an estimate of fiber length was obtained by measuring the distance between the center of the scars of origin and insertion. Such an estimate in *Nothrotheriops* may be fairly accurate because counterparts of these muscles in the tree sloths were long-fibered or largely strap-like. These distances for muscle fiber stretch in *Nothrotheriops* are essentially the maxima, and so these data predict maximum gape. The distance that muscle fibers can stretch without incurring damage is approximately 1.4 times their resting length for parallel fibered muscles and

Table 1. List of specimens examined for this study. Specimen location designations are: LACMHC, Page Museum of La Brea Discoveries; LACM(CIT) Los Angeles County Museum of Natural History received from California Institute of Technology; 192—San Josecito Cave, Nueva Leon, Mexico; 1009—Shelter Cave.

<i>Nothrotheriops shastense</i>		
	Specimen	Catalogue number
	Adult skull	1800-2 (LACMHC 165)
	Adult skull, complete, some teeth	1800-3 (LACMHC 632)
	Adult skull, complete, with teeth	1800-4 (LACMHC 313)
	Adult skull, complete, some teeth	1800-5 (LACMHC 634)
	Adult skull, sectioned midsagittally	1800-6
	Adult skull, posterior only	1800-7 (LACMHC 203)
	Juvenile skull, posterior only	1800-8
	Large juvenile maxillae	1800-9 (LACMHC 641)
	Large juvenile maxillae	1800-10
	Adult skull, complete, all teeth present	1800-11 (LACMHC 208)
	Young juvenile, left maxilla	192-15143 LACM(CIT)
	Juvenile maxilla	1010-S-5-6
	Adult right and half left rami	1801-R-1 (LACMHC 418)
Associated	Adult left ramus fragment with teeth	1801-L-2 (LACMHC 456)
	Adult right dentary, almost complete	1801-R-2 (LACMHC 456)
Associated	Adult left dentary, lacking teeth	1801-L-3 (LACMHC 636)
	Adult right dentary with third molariform	1801-R-3 (LACMHC 636)
Associated	Adult left ramus fragment with teeth	1801-L-4 (LACMHC 638)
	Adult right ramus fragment with teeth	1801-R-4 (LACMHC 637)
Associated	Adult left ramus	1801-L-5 (LACMHC 166)
	Adult right ramus	1801-R-5 (LACMHC 166)
	Adult left ramus with teeth	1801-L-6
	Complete adult mandible with teeth	1801-7 (LACMHC 203)
Associated	Juvenile right ramus with teeth	1009-21749 (LACM)
	Juvenile left ramus with teeth	1009-21750 (LACM)

approximately twice the resting length for multipinnate muscles (Carlsöö, 1942). Quantification of the effect of masticatory muscle orientation on gape was determined using the method of Herring and Herring (1974). This method predicts the distance to which a muscle segment must stretch to enable the animal to achieve a given angle of mandibular rotation. The equation for this calculation is:

$$\left(\frac{L^2}{l}\right) = \frac{a^2 + b^2 - 2ab \cos(\theta + \phi)}{a^2 + b^2 - 2ab \cos \phi}$$

The stretch factor for each muscle (the ratio L/l) is the positive square root of the equation. The values of the variables are: a = length from the muscle origin to the craniomandibular joint (CMJ), b = length from the insertion to the CMJ, ϕ = angle between a and b , L = length of the muscle with the mandible closed and l = length of the muscle with the mandible opened to angle θ .

The teeth used to determine dental structure and mandibular movement patterns were located *in situ* in skulls and mandibles or were assignable to location based upon char-

acters determined in this study. Details of tooth wear were studied using a boom-mounted Nikon binocular dissection microscope, illuminated by a variable intensity Nikon transformer. Teeth were examined under continuously variable magnifications from 8 to 40 $\times$. The examination revealed fine striations, grooves, and irregularities in structure made by tooth-tooth contact, tooth-food contact or damage caused by non-food objects included with foods, or otherwise introduced into the oral cavity.

RESULTS

CRANIAL OSTEOLOGY

Sloth crania have a character suite that distinguishes them from other mammals: (1) reduced, non-tooth-bearing premaxilla; (2) lengthened maxilla; (3) reduced dentitions lacking enamel; (4) persistently growing teeth; (5) often incomplete zygomatic arches; (6) elaborated descending and sometimes ascending zygomatic processes; (7) pterygoid bones with elongate flanges or inflated sinuses; (8) fused mandibular symphyses; and (9) often an elongate premental mandibular

spout. Although all sloths possess some of these characters, no genus shows all, and character combinations differ widely among the three lineages (Mylodontidae, Megalonychidae, and Megatheriidae). Additionally, structural details of many characters differ among groups as well as within a single lineage. Many authors (Simpson, 1945; Scott, 1937; Winge, 1941; Patterson and Pascual, 1972; Stock, 1925; Romer, 1966; Engelmann, 1985; Webb, 1985) have discussed sloth phylogenetic relationships but few studies have focused on the functional implications of cranial structure. Only unusual cranial characters that may contribute to understanding the relationship of structure to function in *Nothrotheriops* are included here.

Premaxilla and Predental Spout

In *Nothrotheriops* the premaxillae are reduced, non-tooth-bearing, and poorly fused both at the midline and maxilla, and consist mostly of a pair of slender, elongated bony processes projecting anteriorly from the maxillae in the palatal plane. None of the specimens examined had intact premaxillae; however, several isolated elements were available. The anterior facial region in *Nothrotheriops* is long because of the maxilla; however, restoration of the premaxillae in proper position further exaggerates this elongation. In contrast, both tree sloths have relatively short faces, with small, arrowhead-shaped premaxillae. Facial shortening is extreme in *Bradypus*, which also has nasal and maxillary bones of reduced length (Naples, 1982).

Correlated with the long anterior nasal region and extremely large nasal opening in *Nothrotheriops* is the elongate predental mandibular spout, which extends the symphyseal area anteriorly. In *Nothrotheriops* the spout portions of the mandibular rami meet to form a channel the width of the distance between the tooth rows through which the sloth could protrude the tongue with little mandibular depression. The extensive use of the tongue by tree sloths in food gathering has been documented (Naples, 1982, 1985a, 1986); this was probably true for *Nothrotheriops* and other ground sloths also. Predental spout morphology varies greatly, including sloths with elongate, narrow spouts (*Nothrotheriops*, *Schismotherium*, *Megatherium*, and *Acratocnus*), short broad spouts (*Glossotherium* and *Lestodon*), short narrow spouts (*Choloepus* and *Megalonyx*) or greatly reduced spouts (*Bradypus*).

Zygomatic Arch and Cranial Ligaments

The zygomatic arch in *Nothrotheriops shastense* shows an ascending process projecting posterodorsally and a descending process projecting ventrally and veering posteriorly toward the tip (Fig. 1A). In comparison, the ascending zygomatic process in *Choloepus* projects more posteriorly than dorsally, although the shape and orientation of the descending process is similar. The ascending process in *Bradypus* is similar in shape and orientation to that of *Nothrotheriops* while the descending process is relatively longer and more slender (Fig. 3F). The squamosal portion of the temporal bone in *Nothrotheriops* is long and slender and almost con-

tacts a notch in the zygomatic bone anteriorly. In life this region was probably an unfused suture. In contrast, a larger space separates the anterior and posterior zygomatic arch processes in *Choloepus* and *Bradypus*. In *Choloepus* the squamosal process shape resembles that of *Nothrotheriops*; in *Bradypus* the squamosal process is more robust.

Judging from tree sloth anatomy a postorbital and zygomatic arch ligament covering the ascending portion of the zygomatic arch in *Nothrotheriops* arose from the postorbital process anteriorly and attached to the upper one-third of the anterior border of the ascending zygomatic process posteriorly (Fig. 1A). Scars indicate that the postorbital ligament origin in *Nothrotheriops* was narrow anteroposteriorly (approximately 20 to 25 mm in available specimens). The posterior edge of the ligament passed from the rear of the postorbital crest to cover the superficial surface of the ascending zygomatic process to the tip. From there it continued posteriorly to attach along the anterior two-thirds of the dorsal border of the squamosal process of the temporal bone, an orientation and arrangement as in *Bradypus*. In *Choloepus* the ligamentous attachments are similar; however, the upper process projects posteriorly, altering the size, shape, and orientation of the ligament.

Structure of the Craniomandibular Joint (CMJ)

In *Nothrotheriops* the glenoid fossa is a shallow and anteroposteriorly elongate groove that conforms loosely to the shape of the articular surface of the mandibular condyle (Fig. 1E). The glenoid fossa permits anteroposterior condylar movement, although, mediolateral condylar movement is restricted. The lateral restriction is produced by a ventral ridge on the squamosal process of the temporal bone. Medially, condylar movement is restricted by the curved temporal surface, buttressed by a thickening at the temporal-pterygoid suture (Fig. 1E). The mandibular condyle is oval with the long axis oriented anteroposteriorly (Fig. 1C–1E). The surface is roughened with small medial and larger lateral articular areas.

The CMJ in *Choloepus* differs from that of *Nothrotheriops* by being wider mediolaterally than anteroposteriorly, with a less pronounced lateral temporal ridge and no medial restriction. The condylar head in *Choloepus* resembles that of *Nothrotheriops*, with two articular surfaces oriented perpendicular to one another, although in *Choloepus* these surfaces are frequently separated by a distinct anteroposterior groove, a derived condition lacking in *Nothrotheriops*.

In *Bradypus* the CMJ generally resembles that of *Nothrotheriops*, although in *Bradypus* the condylar head and glenoid fossa are longer anteroposteriorly and the condyle has a single articular surface (the primitive condition). Both *Nothrotheriops* and *Bradypus* have a medial anteroposterior ridge formed by a raised temporal area. The temporal-pterygoid suture in tree sloths is more ventral than in *Nothrotheriops* and distinct from the medial ridge.

In *Nothrotheriops* the upper and lower tooth rows are equidistant from the CMJ, allowing simultaneous occlusion along the tooth row (Greaves, 1974), and the CMJ is elevated above the occlusal plane. The CMJ location in *Nothrotheriops* dif-

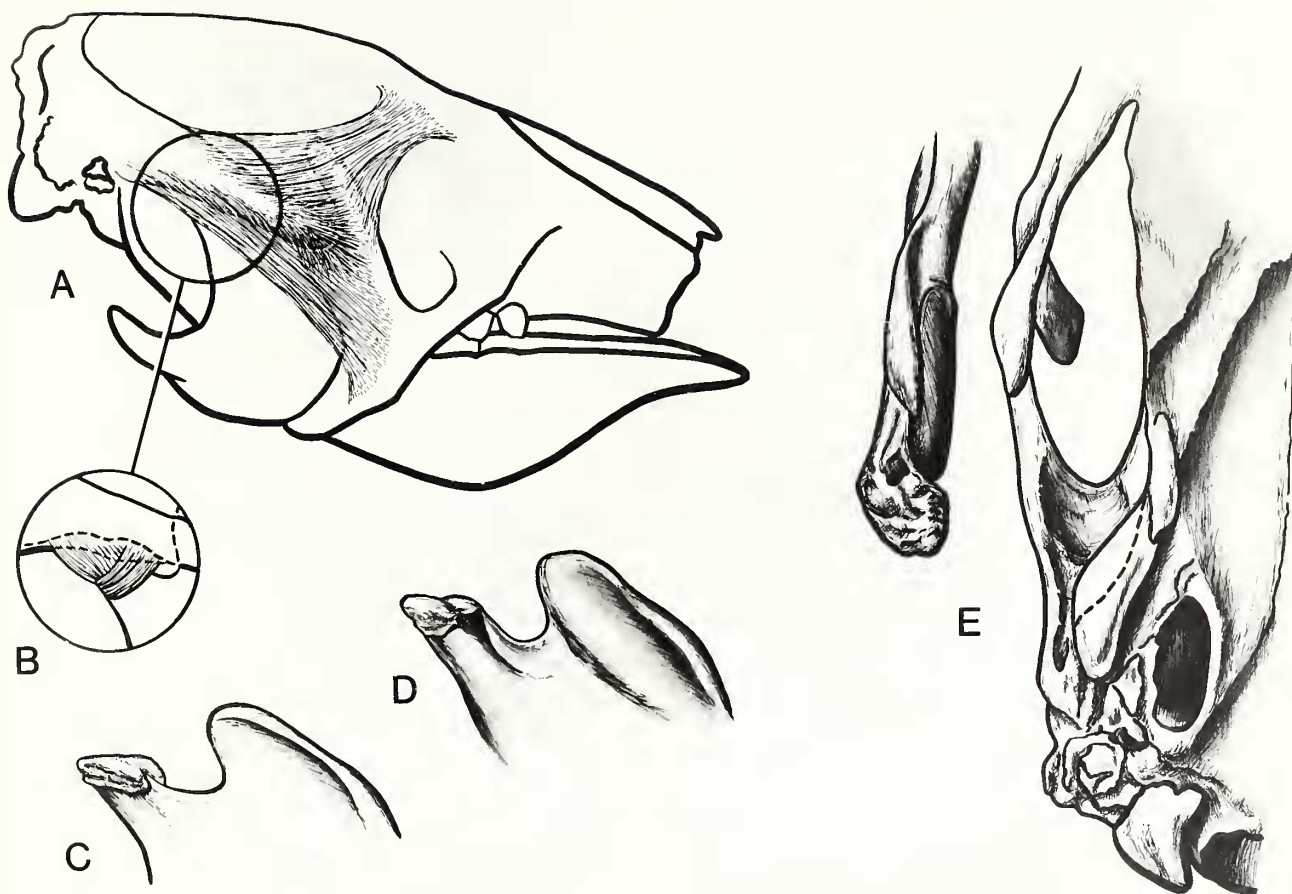


Figure 1. The skull (LACM 1800-1) and mandible (LACM 1801-7) of *Nothrotheriops* in lateral view, showing the ascending and descending processes of the anterior (zygomatic) and the posterior (temporal) portion of the zygomatic arch and connecting ligaments. Although closely apposed, the anterior and posterior zygomatic arch portions do not become fused, even in aged specimens. In some specimens there was probably a thickening of the zygomatic arch ligament between the “zygomatic notch” and the temporal process. The circled area (**1B**) is an enlargement of the craniomandibular joint (CMJ). The temporal process is drawn as though transparent, and the profile of the glenoid fossa shown as a dashed line. The articular capsule ligaments have been restored based upon comparisons with tree sloth morphology. Tree sloths lack an articular disk; therefore none was restored in *Nothrotheriops*. The lateral, medial, and dorsal surfaces of the mandibular condyle are shown in **1C**, **1D**, and **1E**, respectively. The glenoid fossa in ventral view is also shown in **1E**. A dashed line depicts the bony ridge (obscured by the pterygoid sinus inflation posteriorly) that limits the amount of medial movement of the mandibular condyle.

fers from that of *Choloepus* in which the CMJ lies on the occlusal plane but is similar to that of *Bradypus*.

The Pterygoid Region (Fig. 1E)

In *Nothrotheriops* the pterygoid is peculiarly modified when compared to other mammals (Stock, 1925; Turnbull, 1970). Anteriorly the pterygoid has a ventrally expanded flange which shows scars of muscle origin. Posteriorly the bone is inflated and the sinus has a ventral opening. Diversity in pterygoid structure is common among sloths. For example, *Choloepus*

has posteriorly expanded pterygoid sinuses, while flanges in *Bradypus* are ventrally expanded. *Nothrotheriops* is unusual in showing both pterygoid specializations.

DENTAL MORPHOLOGY AND OCCLUSION

In comparison to other herbivorous mammals, sloths have a reduced dentition of unknown ontogeny and homology. Sloth teeth are simple cylinders that grow throughout life. Sloths lack a deciduous dentition (Parker, 1885), and the teeth erupt as small rounded cones prior to birth (Naples,

1982). Sloth teeth lack enamel (Romer, 1966) although differential wear of a harder outer dentine layer and a softer inner one allows formation of "cusps" (Naples, 1981, 1982). As young sloths grow, the conical tooth tips are worn away, exposing a tooth equal in size from occlusal surface to root. Sloth teeth acquire individual characteristics, with basins deepening and cutting edges of the hard outer dentine layer becoming sharper through wear. In aged adults the tooth basins are the deepest and the hard dentine "cusps" the sharpest edged.

In *Nothrotheriops* the dentition is reduced (i.e., specialized) when compared with the tree sloths (Naples, 1982) and with some other related fossil forms such as *Hapalops longiceps* Scott (Stock, 1925) and *Megatherium americanum* (Scott, 1937), because *Nothrotheriops* lacks the typical anterior chisel or peg-shaped teeth. The dental formula for the cheek teeth in *Nothrotheriops* is: $\frac{4}{3}$. The cheek teeth are trapezoidal, and

generally reminiscent of those of tree sloths. A description of cheek tooth structure in *Nothrotheriops* has been presented elsewhere (Stock, 1925), but without discussion of occlusal relationships or wear facet formation patterns. Occlusal relationships are of particular importance in sloths, because the tooth cutting surface shape is determined by mandibular movement patterns wearing the hard and soft areas of dentine (Fig. 2A; Naples, 1981). In *Nothrotheriops* cheek teeth the outer layer of hard dentine is thickest on the posterior faces, only slightly less so on the anterior faces, much thinner on both labial and lingual surfaces, the lingual faces being thinnest (Stock, 1925). In *Nothrotheriops* the mandibular cheek teeth occlude between the maxillary ones, as is typical of most mammals (Romer, 1966). In contrast to most other mammals, however, the reduced number of maxillary cheek teeth in *Nothrotheriops* precede the mandibular ones by half a tooth length, a derived character shared with tree sloths and various other fossil sloth genera such as *Glossotherium*, *Hapalops* (Stock, 1925), *Megalonyx* (Hirschfeld and Webb, 1968), *Mylodon* (Owen, 1842), and *Acratocnus* (Anthony, 1918). During occlusion in *Nothrotheriops* M¹ (notation as in Naples, 1982; M equals molariform and does not imply homology as is usual with such abbreviations and symbols), occludes with M₁; the anterior ridge of M₁ (enclosed within the basin of M¹ during intercuspation) contacts the anterior wall of the M¹ basin when the mandible is shifted anteriorly (Fig. 2B). When the mandible is shifted posteriorly, the large posterior ridge of M₁ contacts the anterior surface of M² (Fig. 2C). The basin and anterior ridge of M₂ fits into the basin of M² when the mandible is located anteriorly; as the mandible shifts posteriorly, the posterior edge of M₂ is brought into contact with the anterior face of M³. Similarly, the anterior edge and basin of M₃ fit within the basin of M³ when the mandible is positioned anteriorly. Only when the mandible is shifted posteriorly does the rear face of M₃ come into contact with the single sloping surface of M⁴. In none of the specimens examined (Table 1) was it possible to maintain simultaneous contact between tooth basins and posterior cutting faces, suggesting that anteroposterior mandibular movement was responsible for wear surface formation (Fig. 2A).

Similar anteroposterior mandibular shifting has been observed in the tree sloths (Naples, 1981, 1982), where mandibular positioning controlled both the proper apposition of cheek teeth and whether or not the anterior teeth occluded for biting or sharpening of wear facets.

The first maxillary cheek tooth (M¹) in *Nothrotheriops* is trapezoidal, with a slightly longer anteroposterior lingual face; it is slightly wider than long anteroposteriorly and smaller than M² and M³ (Stock, 1925; Fig. 2A, 2D). The M¹ is as wide as M⁴, although M⁴ is shorter anteroposteriorly with a single central anterolingually inclined soft dentine basin surrounded by a harder outer dentine layer. The hard outer shell on the anterior face of M¹ in most specimens was chipped and broken away from the softer inner core. This damage may have resulted from: (1) percussion of the anterior edge of M₁ onto the edge of M¹ (which could have weakened support for the anterior edge of the tooth as the central basin deepened), (2) the initial dental handling of sharp or hard-edged foodstuffs, or (3) postdepositional damage to the anterior of the tooth rows. In undamaged specimens, the leading edge of hard dentine lacked anterior or breakage wear facets; frequently, however, a pair of "cusps" was formed on the labial and lingual aspects. The hard dentine shell surrounding the central basin was typically little worn, sharp edged, sometimes pointed anterolabially, and worn away deeply posterolingually. The posterior edge of the hard outer dentine layer was typically worn into a sharp ridge, higher labially than lingually, but arising smoothly anteriorly from the central basin. There was no distinct wear facet facing posteriorly, although the edge of the hard outer dentine curved slightly anteriorly toward the ridge at the crown. Many M¹ specimens showed a slight groove crossing the central basin from midlabial to midlingual indicating the orientation of movements of the hard outer edges of M₁ across the basin (Fig. 2A, 2D).

The M² is about 50 percent larger than M¹, trapezoid shaped, wider than long anteroposteriorly and wider lingually than labially (Fig. 2D). The closest that M² approaches to M¹ is approximately three millimeters. The tooth is oriented squarely in the jaw anteriorly, but because it has a greater lingual length the posterior edge is oblique with the labial "corner" anterior to the lingual "corner." The anterior face of the hard dentine shell of M² shows a facet deeply worn centrally with sharp labial and lingual "cusps" at the "corners."

The M³ is similar in shape to M² although slightly shorter anteroposteriorly (Fig. 2D). The anterior face of the outer layer shows a steep crescent-shaped facet with labial and lingual "cusps" as described in M², but in M³ these "cusps," particularly the lingual, are pointed and sharp edged. The M³ has a central basin which is shallow anteriorly, especially labially, but deeper posteriorly, particularly near the posterolingual "corner" of the tooth. An arcuate groove traverses the basin from anterolabial to posterolingual, becoming more pronounced posterolingually. Lingually, the tooth shell shows the anterior "cusp" mentioned earlier, which continues posteriorly forming a lower ridge. Lingually the tooth shell is more worn posteriorly, steeply from the anterolingual "cusp." Posteriorly on M³ the shell forms a sharp ridge, higher labially

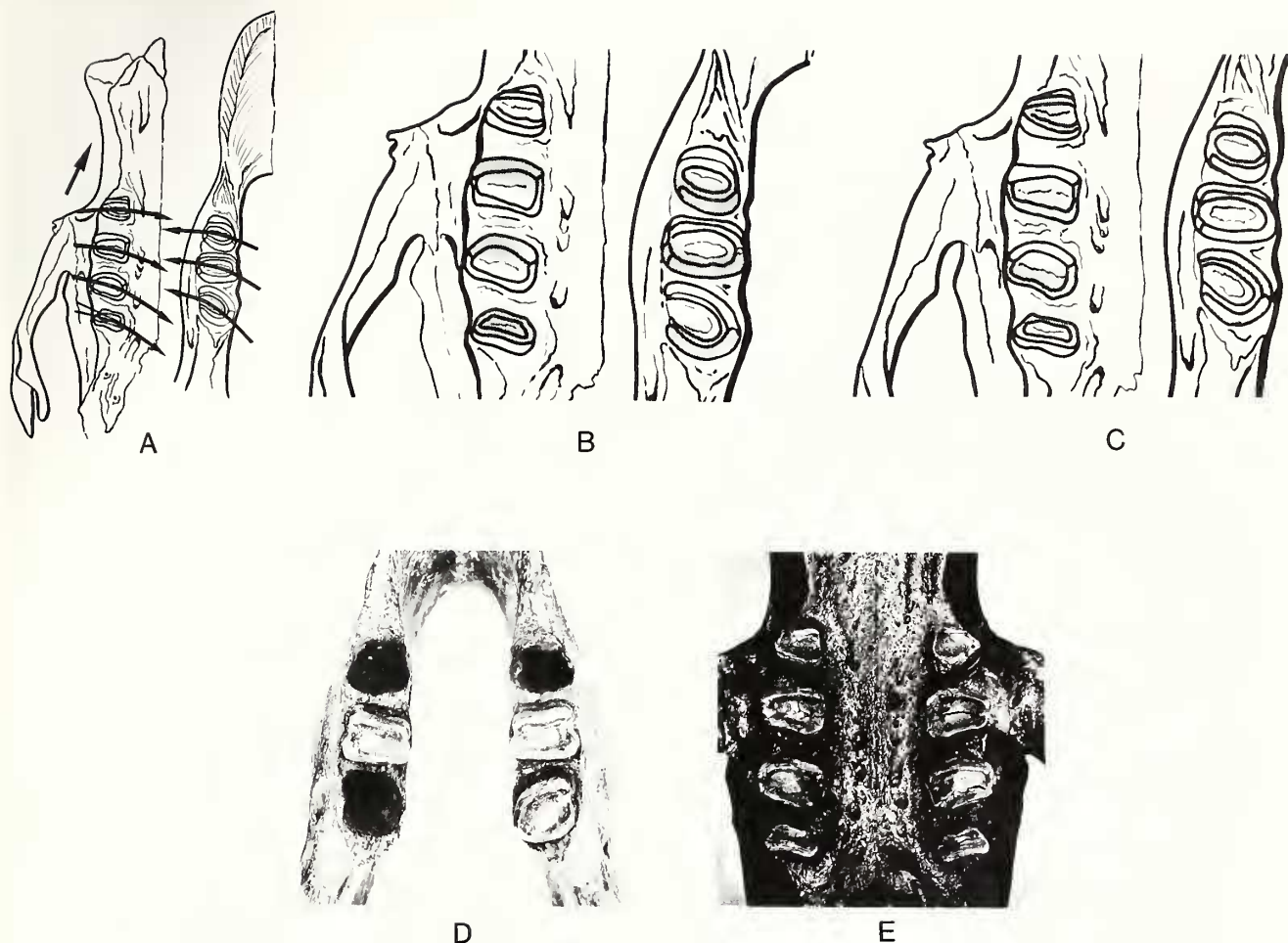


Figure 2. Ventral views of the maxillary and dorsal views of the mandibular tooth rows in *Nothrotheriops* showing the facets worn into the dentition by the anteromedially directed masticatory power stroke (large arrow). The small arrows (2A) show the orientation of wear striations on the teeth. Not all wear facets occluded simultaneously; 2B shows wear facets in occlusion when the mandible is positioned anteriorly, and 2C when the mandible is positioned posteriorly. Occlusal views of the mandibular and maxillary tooth rows are depicted photographically in 2D and 2E, respectively.

than lingually. No wear facet is formed on the posterior face. The M^3 is located slightly further away from M^2 than M^2 is from M^1 (a five millimeter gap at the nearest point along the midline of both teeth).

The M^4 is rectangular in contrast to the more anterior maxillary teeth and wider labiolingually than anteroposteriorly (Fig. 2D). The hard dentine shell is thin on all surfaces of this tooth. Anteriorly, the labial and lingual tooth "cusps" are worn down rather than pointed as in the more anterior cheek teeth, and the dentine shell is convex in the middle. The central basin of M^4 is deeper at the labial and lingual edges and more convex centrally. Posteriorly, the dentine shell has rounded "cusps" at the labial and lingual "corners" and is slightly concave in the center. The M^4 is

separated by approximately the same distance (five millimeters) from M^3 as is M^3 from M^2 . The M^4 is slightly oblique in contrast to the more anterior cheek teeth with the long axis slightly anterolabial to posterolingual.

The first mandibular cheek tooth M_1 is trapezoidal with the anterior aspect smaller than the posterior (Fig. 2E). The anterior face typically is worn, but lacks a distinct facet in the hard outer dentine. Anteriorly, the labial and lingual "corners" lack pointed "cusps," and the face is almost flat labiolingually. The central basin is well worn, deeper antero-lingually than posterolingually. In most specimens a deepened groove traverses the central basin from posterolingual to anterolabial (Fig. 2A, 2E). The labial and lingual faces of the dentine shell are deeply concave and rise to a sharp "cusp"

at the posterior "corners." The posterior face shows a crescent-shaped facet with the wear surface tilted steeply and posteriorly.

The M_2 is similar to M_1 in shape but is broader (Fig. 2E). The anterior face is largely unworn lingually, although a wear facet appears on the anterolabial one-third, forming from contact with the anterolabial "corner" of the central basin of M^2 . Neither the labial nor lingual "corners" of the anterior face of the dentine shell show distinct "cusps." The central basin is shallow lingually, and deepens anterolabially. As in M_1 , a groove crosses from posterolingual to anterolabial. The labial face of M_2 is deeply worn, but rises at the posterior "corner" to form a "cusp." The lingual face is shorter anteroposteriorly than the others and shows a much shallower concavity although there is a prominent "cusp" posteriorly. The posterior face shows a large crescent-shaped "cusp" facing posteriorly. In some specimens the angle at which this face is worn is more steep (i.e., closer to vertical) than that of the corresponding face of M_1 , although there is some variability among specimens.

The M_3 has somewhat more rounded "corners" than do the other teeth, and is set obliquely in the jaw with the longer axis anterolabial to posterolingual (Fig. 2E). The anterior face of this tooth is the most worn of any of the cheek teeth, especially labially. The labial face is deeply worn anteriorly, but rises posteriorly to form a "cusp" at the posterolabial "corner." Lingually the anterior face curves posteriorly, and a single sharp "cusp" is formed posterolingually. The central basin is the largest among the cheek teeth, a rounded triangle with the labial side shorter and flat. As in more anterior cheek teeth, the basin in M_3 is shallower lingually and deepens anterolabially. A groove traverses this basin as in the more anterior teeth, from posterolingual to anterolabial. The posterior face of the hard dentine shell shows a deep, concave, crescent-shaped wear facet with a less steep wear angle than that of the posterior face of M_2 .

An anterior view of correctly occluded *Nothrotheriops* teeth reveals that the tooth rows meet at a slight angle. The axis of the smaller, anterior M^1 is slightly lingual, while the opposite is true for the larger more posterior teeth. In contrast, the mandibular teeth are angled (5–10 degrees) lingually. Growth of the maxillary and mandibular teeth at complementary angles insures that the plane of occlusion is inclined downward labially, as in other herbivorous mammals (Gysi, 1921; Turnbull, 1970; Greaves, 1978, 1980). Because both mandibular and maxillary tooth rows are equidistant from the midline, teeth on both sides of the head occlude simultaneously (Naples, 1981, 1982). In lateral view the maxillary teeth show a distinct anterior tilt while those of the mandible angle slightly posteriorly.

The teeth from several *Nothrotheriops* specimens were examined microscopically for the presence and orientation of wear striations. These teeth were either *in situ* in the mandibles or maxillae or identified according to characters described above. Anterolabial to posterolingual wear striations were discernible in several places, particularly on the hard outer dentine (Fig. 2A). Several authors (Greaves, 1973; Rensberger, 1973; Costa and Greaves, 1981) have shown

that the hard material at the leading edge of the tooth will form a smooth flush transition to the softer material immediately adjacent, while the softer material at the trailing edge will show a step in the transition to the edge of the hard material following it. In *Nothrotheriops* the smooth transitions between hard and soft dentinal interfaces are located posteriorly in mandibular teeth and anteriorly in maxillary teeth indicating an anterior component to the power stroke. Although only arcuate grooves traverse the surfaces of the soft dentine basins their orientation is also consistent with an anteromedially directed masticatory power stroke in *Nothrotheriops* (Fig. 2A).

The grooves in each tooth basin show a flatter arc in M^1 and M_1 and become more arcuate and angled in more posterior teeth (Fig. 2A). As observed by Gordon (1982), the transverse component of mandibular movement is relatively greater for a more anterior than a posterior molar.

CRANIAL MUSCULATURE

The muscles of mastication are supplied by the mandibular branch (V_3) of the trigeminal nerve in mammals, and the branches of this division in the Recent tree sloths reflect the typical mammalian pattern (Naples, 1982, 1985a, 1986). Mandibular nerve branches could not be traced in *Nothrotheriops*; however, the foramen ovale which can be assumed to transmit V_3 is comparable in relative size and position to that in Recent tree sloths.

Masseter Musculature

As in many other mammals (Windle and Parsons, 1899; Schulman, 1906; Toldt, 1906, 1907, 1908; Edgeworth, 1935; Turnbull, 1970) the masseter musculature in sloths is complex and subdivided in a unique pattern (Sicher, 1944), which consists of a *M. masseter superficialis* and a *M. masseter profunda* (Naples, 1985a). In the tree sloths the *M. masseter superficialis* is divided into five parts by tendons and fascial sheets. Distinct scars for origin of these segments occur on the zygomatic arches in Recent sloths, and ridges on the lateral surface of the mandible divide the areas of muscle segment insertion.

In *Nothrotheriops* (Fig. 4A, 4B) the scars are similar in relative size to those of Recent tree sloths. However, some segments differ in relative position from those of one or both of the tree sloths.

***M. masseter superficialis*, part 1 (*M. m. s.-1*).** In *Nothrotheriops* this muscle segment arose from the posterior half of the lateral surface of the descending zygomatic arch process immediately below the anterior zygomatic notch. The notch partially surrounds the anterior tip of the posterior zygomatic arch process (Fig. 4A). The origin is marked by a smooth depression anteriorly, while the posterior edge is slightly roughened and concave (Fig. 4A). The relative positions of the origin in tree sloths are similar to that of *Nothrotheriops*, but the former lack the posterior zygomatic expansion and notch for the anterior tip of the posterior zygomatic arch process. The fibers of *M. m. s.-1* pass posteriorly almost

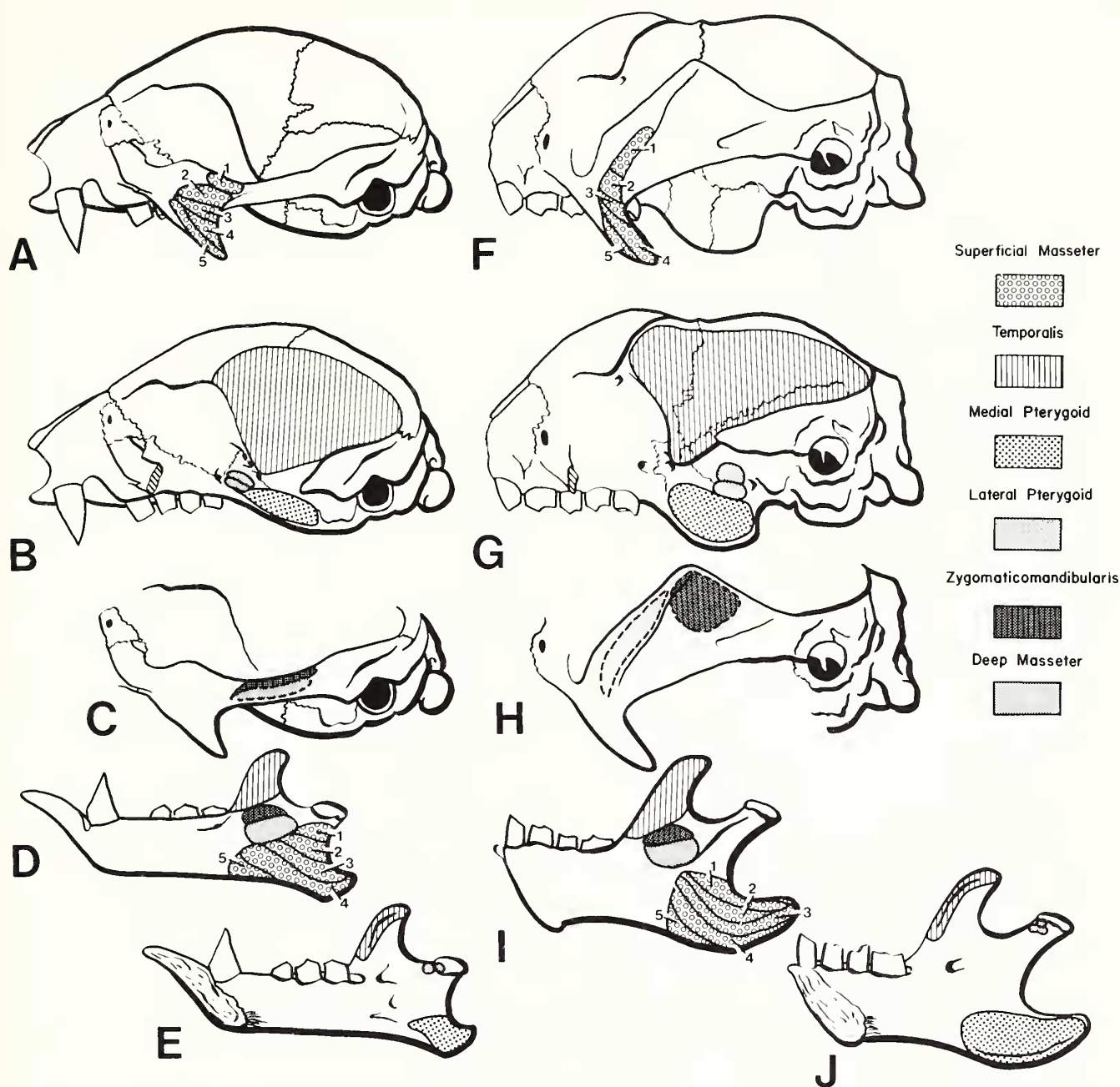


Figure 3. Lateral views of the skull of *Choloepus* (3A–3C) and *Bradypus* (3F–3H) and the mandible of *Choloepus* (3D, 3E) and *Bradypus* (3I, 3J) are shown. The muscle origins are from the skulls and the insertions on mandibles. The key to the right of the drawing shows the muscles identified by different patterns.

parallel to the occlusal plane of the tooth row (defined as horizontal in future discussion) to insert into a rough surfaced depression laterally on the angular notch in *Nothrotheriops* (Fig. 4B).

M. masseter superficialis, part 2 (*M. m. s.-2*). In *Nothrotheriops* this muscle segment arises from a smooth depression on the posterior half of the zygomatic process ventral to that of *M. m. s.-1* (Fig. 4A). Although the origin may have been somewhat tendinous, muscle fibers probably also arose

directly from the depression as in the tree sloths. The fibers passed posteriorly to insert into a depression on the lateral mandibular surface ventral and anterior to the insertion of *M. m. s.-1* (Fig. 4B). This arrangement is similar in *Choloepus* and *Bradypus* (Fig. 3A, 3D, 3F, 3I). In the tree sloths the dorsal segments of the *M. m. s.* are partially covered by fibers of more ventral segments, especially near the insertions; the muscle has been restored similarly in *Nothrotheriops* (Fig. 4C).

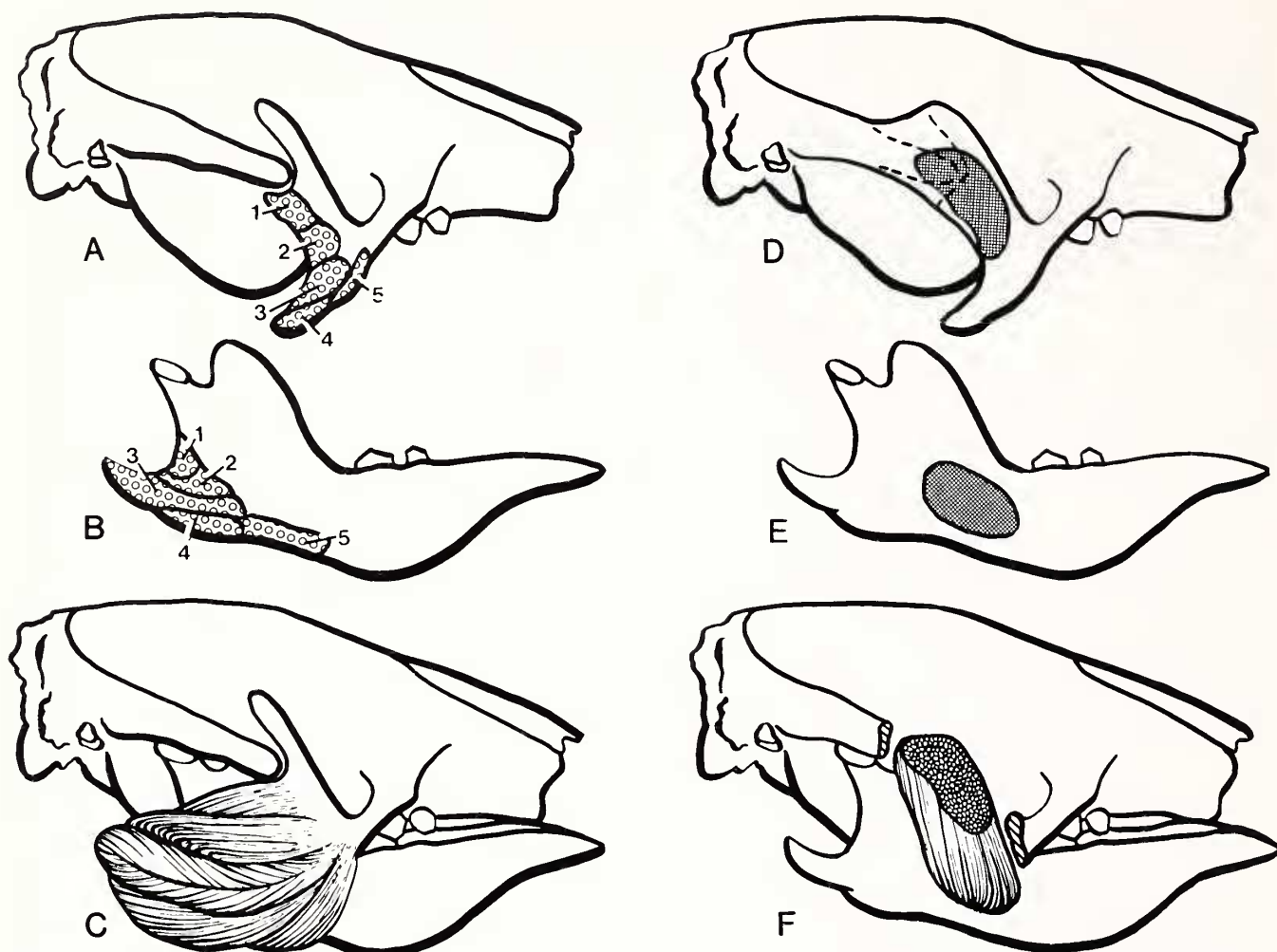


Figure 4. The skull and mandible of *Nothrotheriops* shows the origins (4A), insertions (4B) and a reconstruction (4C) of the five portions of the *M. masseter superficialis*, the origin (4D), insertion (4E), and a reconstruction (4F) of the *M. masseter profunda*. The origin of the *M. m. p.* is from the deep surface of the zygomatic arch and connecting ligaments and is indicated as transparent (4D) and (4F).

***M. masseter superficialis*, part 3 (*M. m. s.-3*).** In *Nothrotheriops* the scar of origin is a smooth depression ventral to that of *M. m. s.-2*, and larger than those of both dorsal segments (Fig. 4A). This was the largest segment of *M. m. s.* in *Nothrotheriops*, with fibers passing horizontally and posteriorly to insert onto an elongate roughened ridge on the lateral mandibular surface ventral to the center of the coronoid process and posteriorly to the angular process tip (Fig. 4B). Because of the relative position of the origin of this muscle segment, it has been restored as bipinnate as are *M. m. s.-3* in *Choloepus* and *Bradypus*. In *Choloepus*, the insertion of *M. m. s.-3* lies dorsal to the angular process tip and the muscle segment is relatively smaller. In *Bradypus* *M. m. s.-3* inserts on the angular process, encompassing the tip, and is relatively larger than in *Choloepus* but smaller than the *M. m. s.-3* restored in *Nothrotheriops* in accord with the differences in proportion between the areas of origin and insertion in the tree sloth genera. The fiber direction of *M. m. s.-3* in

tree sloths is approximately parallel to the plane of the cheek teeth, as is also true in *Nothrotheriops*.

***M. masseter superficialis*, part 4 (*M. m. s.-4*)** (Fig. 4A–4C). In *Nothrotheriops* this segment originates from the most ventral depression on the descending zygomatic process. A ridge bounds this depression dorsally and anteroventrally, forming a thickened roughened area along the ventral edge of the descending zygomatic process tip, and a thin, smooth, sharp posterior edge (Fig. 4A–4C). Muscle fibers passed horizontally from the posterior edge of the descending zygomatic process to insert on a flattened and roughened ventrolateral surface of the elongate mandibular angular process anterior and ventral to the tip (Fig. 4B). In *Nothrotheriops* *M. m. s.-4* formed much of the lower border of *M. masseter superficialis*, and therefore its bulk affected the cranial profile. In *Choloepus* and *Bradypus* this muscle segment arises by a single tendon, as was likely in *Nothrotheriops*. In tree sloths the segment is multipinnate with many internal fascicles, as is

logical in *Nothrotheriops*, considering the orientation and probable large size of the segment.

M. masseter superficialis, part 5 (M. m. s.-5). In *Nothrotheriops*, this segment arose from the leading edge and elongate anteroventral depression laterally on the descending zygomatic process. The origin was bounded by raised ridges dorsally and posteriorly and by thickened jugal process edges anteriorly and ventrally (Fig. 4A). Fibers of this segment passed ventrally (approximately 45 degrees from horizontal) and posteriorly to insert on the lateral surface of the mandibular ramus anterior to the insertion of *M. m. s.-4*. Additionally, these fibers wrapped around the thickened ventral ramal edge carrying the insertion approximately 8 mm onto the medial surface. In both Recent tree sloths, and probably in *Nothrotheriops*, *M. m. s.-5* formed the "bulge" at the anterior edge of *M. masseter superficialis*. In all three sloths, the anterior limit of the insertion of *M. m. s.-5* is marked by a depression on the lateral surface of the mandibular ramus anterior to the last lower molariform tooth. The depression is crescent-shaped in *Choloepus* and *Bradypus* (with posteriorly facing points) and in *Nothrotheriops* the depression edges are straight and angle posteroventrally. In tree sloths this segment is structurally complex with many tendons and fascial planes. A similarly complex structure would have been especially important in *Nothrotheriops*, as pinnation enhances the ability of a muscle to stretch although at the expense of force (Herring, 1975), and this anteriormost segment with a short distance from origin to insertion would limit the degree to which the mouth could open.

The structure, fiber arrangement, and size of the superficial masseter musculature in *Nothrotheriops* are generally similar to those of *Choloepus* and *Bradypus* (Fig. 4C; Naples, 1982). However, the overall line of action is more horizontal than in tree sloths, and affects the pattern of mandibular movement in mastication. Another difference between the masseter complex in *Nothrotheriops* and the tree sloths is that the orientation of the line of action of *M. m. s.-5* in *Nothrotheriops* departs greatly from that of the other segments. This arrangement may also affect the masticatory pattern, allowing *Nothrotheriops* to move the mandible with additional force in an anterior direction (Naples, 1985a; Fig. 7A).

M. masseter pars profunda (M. m. p.) (Fig. 4D–4F). In *Nothrotheriops* this muscle arose from the medial surface of both ascending and descending zygomatic processes and medially from the posterior portion of the zygomatic arch. The origin sites on the zygomatic are smooth depressions, while the squamosal origin of *M. m. p.* is roughened. Fibers insert ventrally in a smooth oval depression bounded by raised ridges on the lateral surface of the mandible dorsal to the site of insertion of *M. m. s.-5*. This muscle was probably thin as is true in *Choloepus* and *Bradypus* with many long fibers passing from origin to insertion, but few tendons. The space between the descending zygomatic process and the mandibular ramus in *Nothrotheriops* is relatively narrower than in *Bradypus* or *Choloepus* and probably also restricted the thickness of the *M. m. p.* In *Choloepus*, the *M. m. p.* is relatively much smaller than in *Nothrotheriops*, because of the more vertical orientation and expansion of the zygomatic

arch and the more anteriorly expanded insertion on the mandibular ramus in *Nothrotheriops*. However, both *Nothrotheriops* and *Choloepus* share the direction of line of action for this muscle defined as primitive by Turnbull (1970; Fig. 7A). The *M. m. p.* in *Bradypus* is comparable in relative size to that of *Nothrotheriops*, although the lines of action differ greatly; that of *Bradypus* passes posterodorsally, as a result of the extreme shortening of the face, a derived condition in this genus (Naples, 1985a).

The Temporalis Musculature

In *Nothrotheriops* muscle scars suggest that the temporal mass was relatively small, and undivided. *Nothrotheriops* lacks a sagittal crest, although the dorsal edges of the *M. temporalis* origin arise only 15 mm apart and cover most of the lateral and dorsal aspects of the frontal and parietal bones (Fig. 5A). The entire margin of the origin is marked by a roughened ridge, anteriorly from the widest part of the postorbital process and supraorbital foramen, dorsally and posteriorly to curve ventrally near the caudal border of the parietal bone to join the dorsal ridge of the temporal squamosal process. Muscle fibers also arose from the squamosal process medially, and the groove between it and the temporo-parietal surface of the skull. The ventral border of the origin of *M. temporalis* was deep to the zygomatic arch from a roughened ridge passing anteriorly along the temporo-parietal suture and then to the frontal. The ridge continues anteriorly, and expands ventrally to form a partial roof over the optic nerve foramen deep to the anterior edge of the zygomatic arch. The raised surface then curves upward toward the postorbital process. The muscle probably filled the posterior third of the orbital fossa. The entire surface of the *M. temporalis* origin is roughened for attachment of many small tendons or muscle fascicles. Fibers passed ventrally to attach to the lateral, anterior, and medial surfaces of the mandibular coronoid process. Laterally, the coronoid process insertion shows a pronounced outwardly curved ridge, especially dorsally (Fig. 5C). The line of action of *M. temporalis* in *Nothrotheriops* was approximately 45 degrees to the occlusal plane as in other mammals (Turnbull, 1970; Naples, 1985a), permitting both mandibular elevation and retraction (Fig. 7A, 7B). The *M. temporalis* in *Nothrotheriops* and *Choloepus* are similar in relative size, shape, and line of action although an *M. temporalis superficialis pars zygomatica* as in *Choloepus* cannot be demonstrated in *Nothrotheriops*. The structure of *M. temporalis* in *Nothrotheriops* resembles that of *Bradypus* in relative size and shape, but the line of action in *Bradypus* differs greatly, and has been described as a derived character for this sloth (Naples, 1985a; Fig. 3B, 3D, 3G, 3I, 3J).

M. zygomaticomandibularis (=M. temporalis superficialis pars zygomaticomandibularis; = M. z.) (Fig. 5F–5H). Evidence for the origin and insertion sites of this muscle is less clear in *Nothrotheriops* than for muscles discussed previously. However, the ascending zygomatic process is large in *Nothrotheriops*, and has a roughened medial surface which could have been the anterodorsal origin for the *M. z.* The ligamentous connections as restored (Fig. 1A) would have

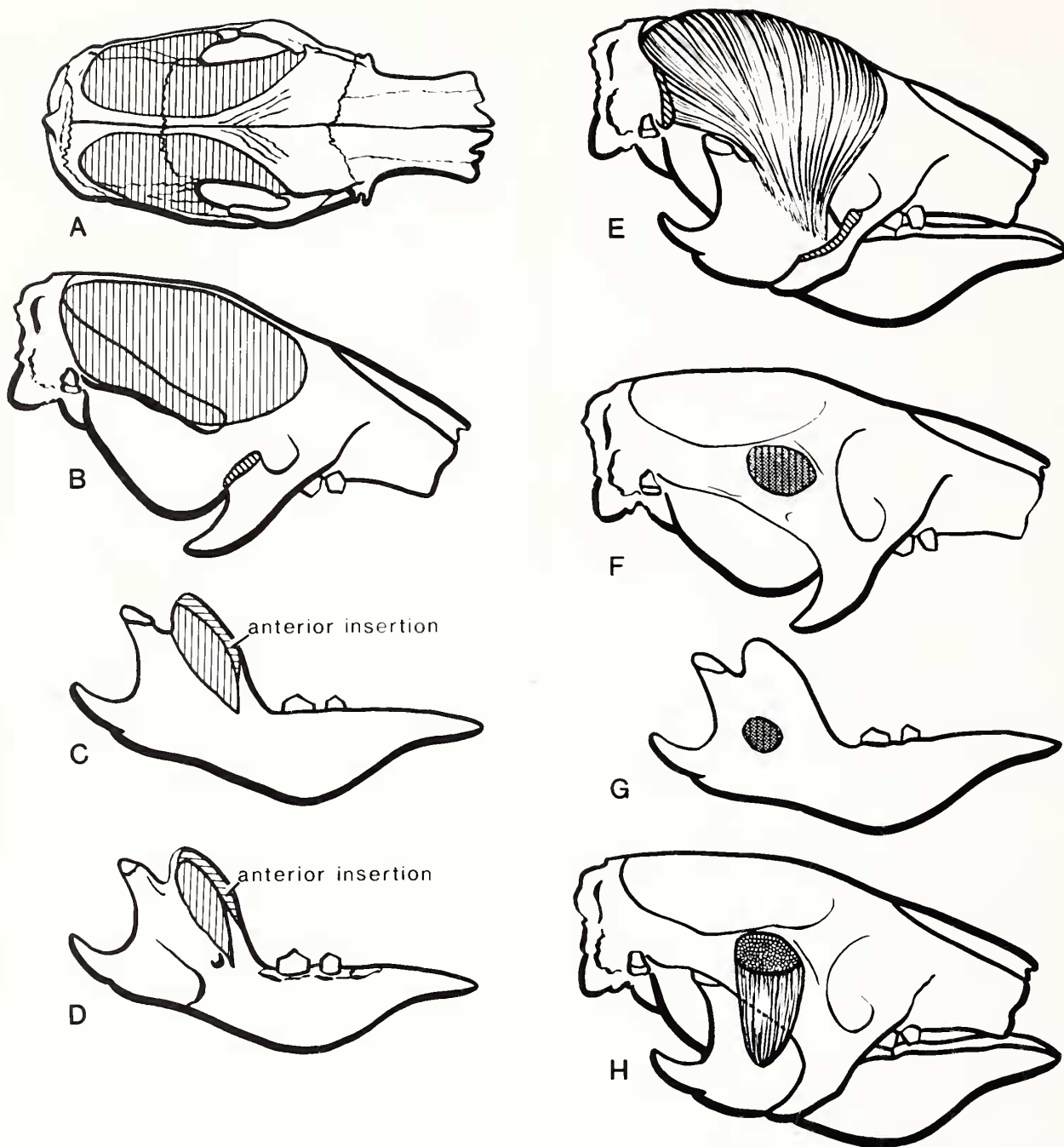


Figure 5. Outlines of skull and jaw of *Nothrotheriops*. The skull (**5A**, **5B**) and mandible (**5C**, **5D**) of *Nothrotheriops* shows the origin dorsally (**5A**) and laterally (**5B**) of the *M. temporalis*, the lateral and medial aspects of the insertion (**5C** and **5D**, respectively) and a reconstruction of the muscle (**5E**). To show the reconstructed muscle fibers which pass deep to the zygomatic arch and its ligaments a portion of the zygomatic arch has been removed. The origin (**5F**), insertion (**5G**), and reconstruction (**5H**) of the *M. zygomaticomandibularis* are shown. The origin of the *M. z.* is from the deep surface of the zygomatic arch and its ligaments which are shown as transparent in **5F** and **5H**.

increased the origin site area. Evidence favoring reconstruction of this muscle derives from its presence in both tree sloths, although in *Choloepus* the muscle is smaller, restricted in origin from a horizontal zygomatic arch as in most other mammals (Edgeworth, 1935; Turnbull, 1970). In *Bradypus*,

the arch was reoriented (another derived condition) more vertically, greatly increasing the origin of the *M. z.* (Fig. 3H, 3I). The zygomatic arch orientation in *Nothrotheriops* resembled that in *Bradypus* (Naples, 1985a), although less extreme; therefore the muscle had a size and orientation between those

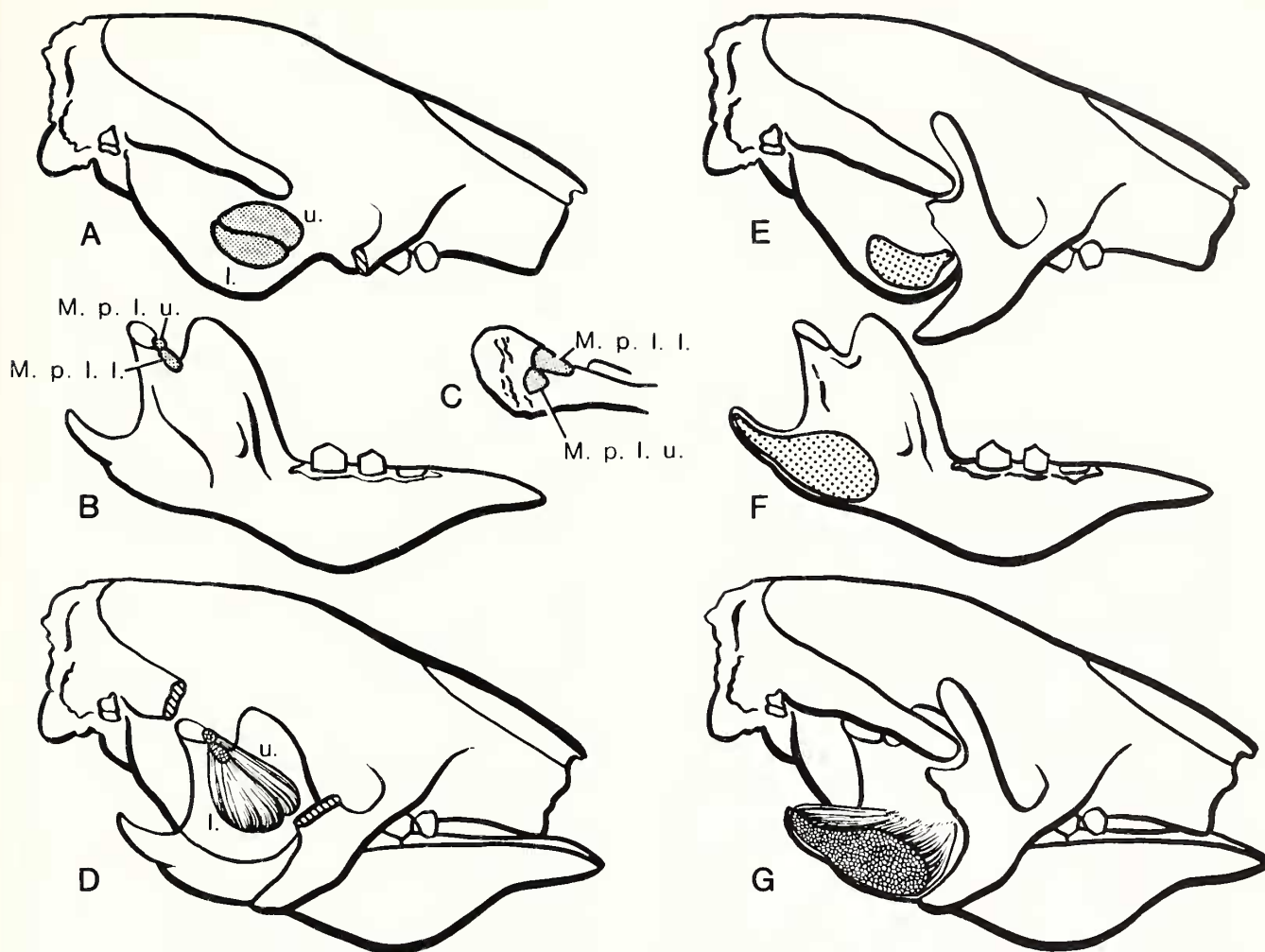


Figure 6. The origin (6A), insertion in lateral view (6B), in dorsal view (6C), and a reconstruction (6D) of the *M. pterygoideus lateralis* (*M. p. l.*) upper and lower portions (*M. p. l. u.* and *M. p. l. l.*, respectively) are shown. In (6D) the zygomatic portion of the zygomatic arch has been removed and the mandible is shown as transparent. The origin (6E), insertion (6F), and reconstruction (6G) of *M. pterygoideus medius* are shown, and as in 6D, the mandible in 6G is transparent and the muscle inserts upon the medial surface.

of the two tree sloths. Fibers of this muscle in *Nothrotheriops* passed ventrally and slightly posteriorly to insert posterodorsally to fibers of *M. m. p.* (Fig. 4D–4F). As observed in *Nothrotheriops* for *M. m. p.* the mediolateral distance between zygomatic arch and skull wall is small, restricting this muscle in mediolateral thickness (Fig. 5A).

The Pterygoideus Musculature (Fig. 6)

In sloths this muscle mass is large relative to that of other mammals, although the division number and muscle fiber arrangement is not unusual (Edgeworth, 1935; Toldt, 1906, 1907, 1908; Turnbull, 1970; Naples, 1985a).

***M. pterygoideus lateralis*, upper part (*M. p. l. u.*).** In *Nothrotheriops* this muscle arose from an oval lateral fossa on the ventrally elongated pterygoid flange with the long axis an-

teroventral to posterodorsal. The muscle passed posterodorsally to insert into a central depression of the anterior edge of the articular condyle at its neck (Fig. 6B, 6C). In *Choloepus* and *Bradypus* this muscle arises and inserts similarly; the origin is more distinct in *Nothrotheriops*. *Choloepus* and other mammals (e.g., carnivores, insectivores, and artiodactyl herbivores, Turnbull, 1970) show the typical line of action. However, in *Nothrotheriops* the posterodorsal fiber direction is derived, a condition also seen in *Bradypus*, although the line of action in the latter sloth is even more vertical (Naples, 1985a; Fig. 3B, 3D, 3G, 3J). In the tree sloths the muscle is thick and fleshy, divided by few internal fascial planes as was assumed in *Nothrotheriops*.

***M. pterygoideus lateralis*, lower part (*M. p. l. l.*).** In *Nothrotheriops* this segment arose from an elongated oval fossa posteroventral to the larger rounder oval origin of *M. p. l. u.*

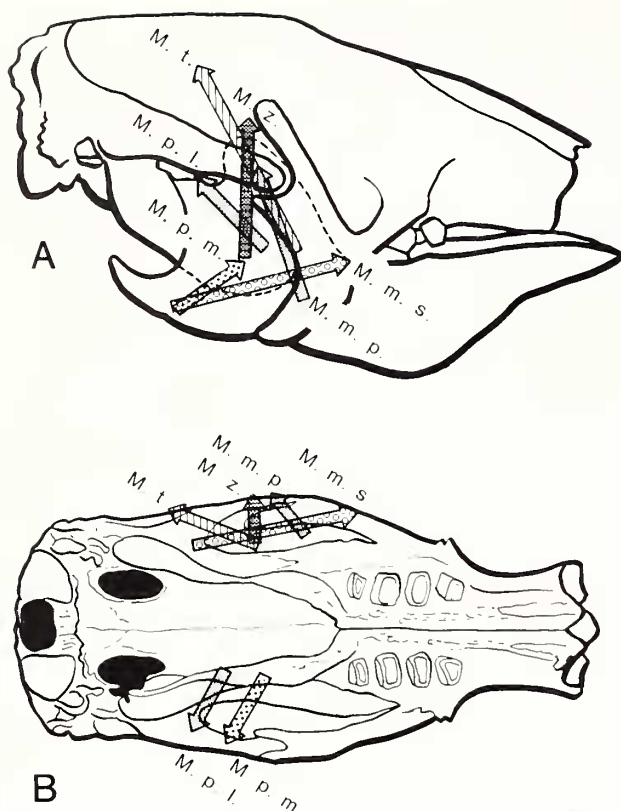


Figure 7. The skull and mandible in lateral view (7A) and in ventral view the skull only (7B) of *Nothrotheriops*, show the lines of action of the muscles of mastication. Muscle names and their abbreviations are: *M. masseter superficialis* (*M. m. s.*), *M. masseter profunda* (*M. m. p.*), *M. temporalis* (*M. t.*), *M. temporalis pars zygomaticomandibularis* (*M. z.*), *M. pterygoideus lateralis* (*M. p. l.*), and *M. pterygoideus medius* (*M. p. m.*). The length of the lines reflect the muscle force resultants.

(Fig. 6A–6D). The line of action was posterodorsal also, but more vertical than that of the upper division. The *M. p. l. l.* inserted into the dorsal edge of a flattened oval depression at the anteromedial edge of the condylar neck and anteroventrally along the medial surface of the condylar notch. In *Choloepus* and *Bradypus* (Fig. 3B, 3D, 3G, 3J) this muscle segment is fleshy, and probably was also in *Nothrotheriops*. The posterodorsal line of action in *Nothrotheriops* differed from that in *Choloepus*, but was similarly, if less vertically oriented than in *Bradypus*. The *M. p. l. u.* and the *M. p. l. l.* were separate and probably intermediate in relative size in *Nothrotheriops* compared to the relatively small *M. p. l.* in *Choloepus*, and the relatively large one in *Bradypus* (Figs. 3B, 3E, 3G, 3J, 6A–6D).

In *Choloepus* the *M. p. l.* pulled anteromedially with a very small vertical force component. In *Bradypus* the medial force component is greater than the anterior, but instead of being directed dorsally the vertical force is ventrally directed. However, the *M. p. l.* functioned comparably in both Recent

sloths because the downward component coupled with other muscular forces pulling the mandibular condyle anteromedially (i.e., masseter and medial pterygoid musculature) depresses the condylar head slightly. In *Bradypus* the condylar head is pushed against an enlarged bony stop on the medial glenoid surface. Once in this position bony resistance cancels further downward condylar motion, presuming the muscles are active on both sides of the head simultaneously (Gysi, 1921; Herring et al., 1979); this mechanism then prevents condylar dislocation (Naples, 1985a). The medial glenoid surface in *Nothrotheriops* had an even better bony stop than in *Bradypus*; combined with a similar lateral bony stop, condylar movement in *Nothrotheriops* was more restricted mediolaterally than in *Bradypus* (Figs. 1E, 6C).

***M. pterygoideus medius* (*M. p. m.*).** In *Nothrotheriops*, this muscle arose laterally from the elongated pterygoid flange, anterior to the inflation ventral and slightly posterior to the origin of *M. p. l.* (Fig. 6E). Fibers passed posteroventrally to insert medially into a fossa outlined by sharp ridges on the mandibular body and angle (Fig. 6F, 6G). The *M. p. m.* in *Nothrotheriops* was relatively larger than in *Choloepus*, and had an anteroposteriorly directed line of action, similar to that in *Bradypus* (Fig. 7A, 7B; Naples, 1985a). However, the *M. p. m.* in *Nothrotheriops* was relatively smaller than that of *Bradypus*, and the mandibular angle less elongate posteriorly. In the tree sloths the *M. p. m.* is largely undivided by internal fascial planes; lack of attachment ridges for tendons at the insertion suggests that this was also true for *Nothrotheriops*.

ESTIMATION OF GAPE

The degree to which sloths can gape affects the manner in which they feed and is determined by the following factors: (1) mandibular shape and length, (2) position, orientation, and shape of the craniomandibular joint, and (3) orientation, shape, and length of the segments of the muscles of mastication.

Restrictions limiting mandibular opening were found to be few up to a gape of approximately 40 degrees where the mandible would clearly be dislocated and the posterior surface of the angular process would “bump against” the pterygoid sinuses. In addition to limits imposed upon gape by osteology, it has been suggested that muscles cannot be stretched more than twice their resting length without incurring damage (Carlsöö, 1942). The distance to which masticatory muscle components in *Nothrotheriops* would be stretched at gapes of 20, 25, 30, and 40 degrees was determined using the method of Herring and Herring (1974; Table 2). The analysis suggests that the lowest superficial masseter segment (*M. m. s.-5*) would be overstretched at a gape greater than 25 degrees. The medial pterygoid is the next muscle or segment most limiting, allowing only a few additional degrees of gape. The other muscles of mastication did not appear to limit gape up to 40 degrees, the point at which the mandible would become dislocated at the CMJ. *Choloepus* shows a somewhat wider gape (60 degrees), but *Bradypus* has about the same (40 degrees). In both genera dislocation at the CMJ

Table 2. The cranial muscles, divisions, and abbreviations used in this study and the amount of stretch of each muscle segment when the mouth is opened to various degrees of gape. Multipinnate muscles may stretch up to two times their resting length without incurring damage; therefore only stretch factors over 2.00 would be limiting. For *Nothrotheriops*, the *M. m. s.-5* could then be overstretched at gapes greater than 25 degrees, with the *M. pterygoideus medius* only slightly less limiting. Muscles stretched more than twice their resting length for each gape measurement are marked with an asterisk (*).

Muscle	Divisions	Abbreviation	Measurement	Degrees of gape			
			location	20	25	30	40
<i>M. masseter superficialis</i>							
	part 1	<i>M. m. s.-1</i>		1.36	1.45	1.45	1.69
	part 2	<i>M. m. s.-2</i>		1.32	1.40	1.47	1.62
	part 3	<i>M. m. s.-3</i>		1.22	1.28	1.33	1.42
	part 4	<i>M. m. s.-4</i>		1.42	1.52	1.53	1.82
	part 5	<i>M. m. s.-5</i>		1.75	1.96	2.18*	2.63
<i>M. masseter pars profunda</i>		<i>M. m. p.</i>		—	—	—	—
<i>M. temporalis</i>		<i>M. t.</i>	<i>M. t.</i> (anterior)	1.37	1.47	1.58	1.79
			<i>M. t.</i> (middle)	1.22	1.28	1.33	1.35
			<i>M. t.</i> (posterior)	1.03	1.04	1.05	1.05
<i>M. zygomaticomandibularis</i> (= <i>M. temporalis superficialis pars</i> <i>zygomaticomandibularis</i>)		<i>M. z.</i>		—	—	—	—
<i>M. pterygoideus lateralis</i>	upper part	<i>M. p. l. u.</i>		1.02	1.03	1.04	1.06
	lower part	<i>M. p. l. l.</i>		1.06	1.08	1.09	1.12
<i>M. pterygoideus medius</i>		<i>M. p. m.</i>		1.74	1.90	2.12*	2.47

and overstretching of the superficial masseter segment (*M. m. s.-5*) is the limiting factor.

DISCUSSION

The four data sets considered in this analysis are: (1) cranial osteologic characters unique to or mainly restricted to *Nothrotheriops*, (2) dental characters and reconstruction of dental function, (3) reconstruction of the structural and functional capabilities of the masticatory musculature and other soft cranial structures, and (4) digestive efficiency as estimated from analyses of sloth dung. These independent lines of evidence should make it possible to: (1) differentiate plesiomorphic, apomorphic, and autapomorphic cranial characters, (2) determine the functional abilities and limitations common to the three sloth lineages, and (3) reconstruct the function and evolutionary history of the nothrotherian ground sloths.

Premaxilla and Predental Spout

In all sloths the premaxilla is reduced (Winge, 1941; Romer, 1966; Naples, 1982) usually to an arrowhead shaped element that does not contact the nasal bones. In *Nothrotheriops* these elements are elongate, slender, unfused at the midline and extend as far as anteriorly the elongate mandibular predental spout. These processes add to the elongate face in *Nothrotheriops*, a condition also evident from the long maxillae. Because predental spouts occur in all three ground sloth lineages they are considered primitive in *Nothrotheriops* (Stock,

1925; Winge, 1941; Naples, 1982, 1985a). The long face in this sloth was probably also augmented by a large amount of soft tissue as was suggested by the large sized nasal openings. Even though tree sloths, particularly *Bradypus*, have short faces, they have large nasal cartilages and much other soft rhinarial tissue anterior to the premaxillae to control the flexible upper lip (Naples, 1982). Therefore *Nothrotheriops* may also have had a flexible upper lip to aid in food manipulation. Few earlier cranial reconstructions of *Nothrotheriops* included premaxillae or suppose a large amount of soft tissue anteriorly. Therefore, the typical earlier facial reconstruction in this sloth is probably too short (Fig. 8).

Structural Relationships of the Zygomatic Arch, CMJ, and Cranial Ligaments

A zygomatic arch with ascending and descending processes and an elongate temporal squamosal process are typical for sloths. In *Nothrotheriops* these processes are unfused but closely approximated and probably connected by a thickened zygomatic arch ligament. An incomplete zygomatic arch is common among sloths, particularly among the smaller genera such as *Bradypus* and *Choloepus* and the megalonychids. However, the zygomatic arch in *Nothrotheriops* is unusual because of the closely apposed anterior and posterior portions, with a notch in the zygomatic bone between ascending and descending processes to receive the anterior end of the squamosal process. The zygomatic notch increases the surface area where the zygomatic arch processes approximate, providing more attachment area for the short joining liga-

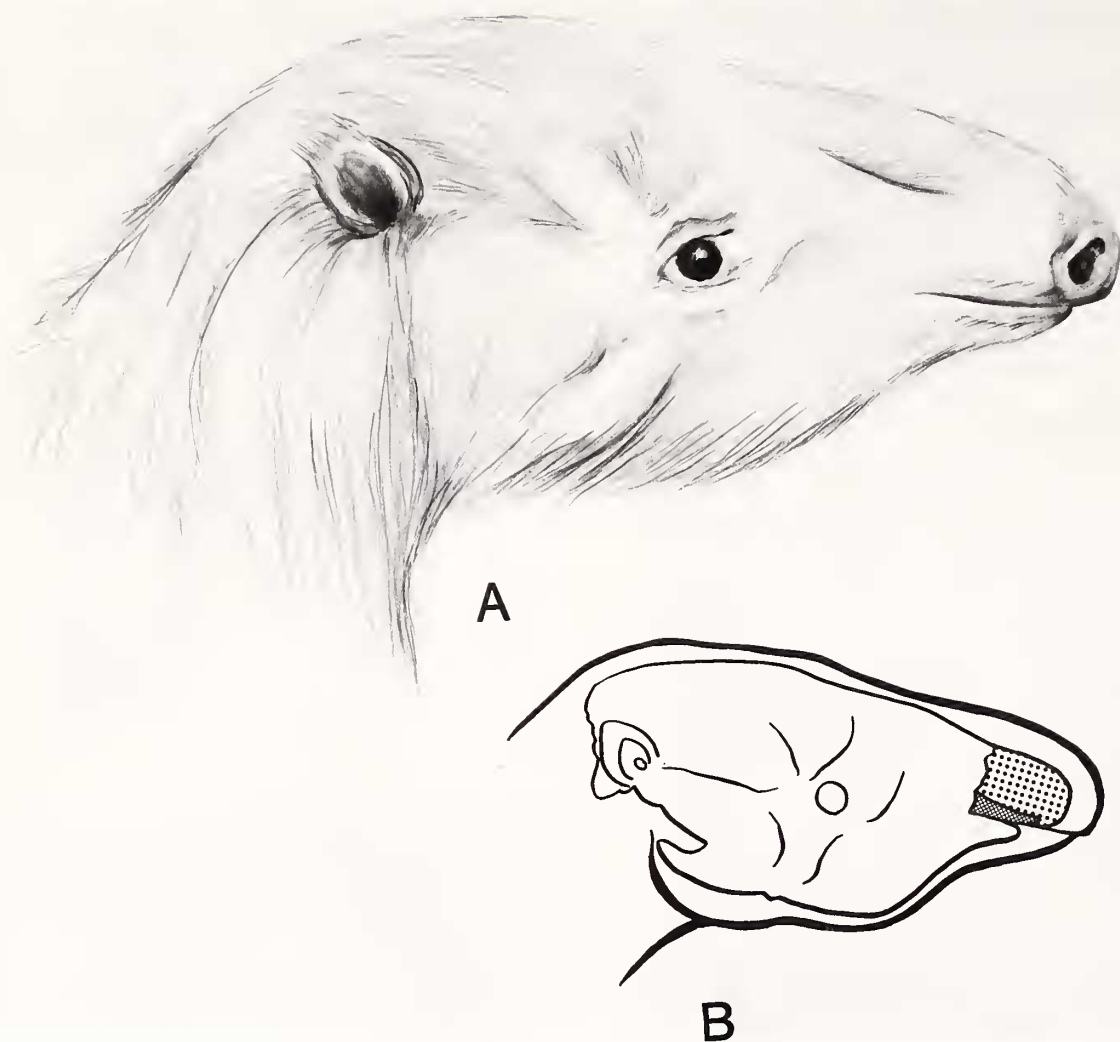


Figure 8. Reconstruction of the appearance of the head of *Nothrotheriops* in lateral view (8A) and the skull and nasal cartilages are outlined in (8B).

ments. In small sloths the zygomatic arch gap is larger, and in most sloths equal to or greater in size than in *Nothrotheriops*, and the anterior and posterior portions are fused. *Nothrotheriops* is unique in having the two parts closely apposed, but unfused, an autopomorphy confined to the nothrotheres.

As in *Bradypus* (Naples, 1982, 1985a), the ascending zygomatic process permits expansion of the origin area of *M. temporalis pars zygomaticomandibularis* and *M. masseter profunda* and allows these muscles a more vertical line of action than would have been possible otherwise. Improvement of the mechanical advantage of the muscles in *Bradypus* correlates with a CMJ above the occlusal plane. An elevated CMJ determines that the masticatory movement pattern emphasizes the anteroposterior component of mandibular movement as also indicated by wear facet orientation, striations, and the position of steps in the transition areas between hard and soft dentine. Anatomical changes to

allow more anteroposterior movement during mandibular closing were possible for *Bradypus* because this sloth had lost the elongate caniniform teeth that require precise dorsoventral alignment and minimized anteroposterior movement. This biomechanically advantageous masticatory muscle arrangement and CMJ height was unattainable for *Choloepus*, which retains elongate caniniform teeth. However, the lesser masticatory mechanical advantage must have been offset by the importance of retaining useful caniniform teeth as demonstrated by *Choloepus* using these teeth for threat displays, active defense, and for piercing and cutting food items. These differences suggest that the two tree sloth lineages either were subject to different selective pressures or initially were very different in cranial morphology. Because tree sloths share the same habitat, the latter is probably correct, and supports the idea that *Bradypus* and *Choloepus* arose from distantly related ground sloth lineages (Engle-

mann, 1985; Webb, 1985). However, for this study, functional questions concerning *Nothrotheriops* have been analyzed based upon comparisons with both *Bradypus* and *Choloepus*.

Wear facet orientation, dental striations, the presence or absence of steps between hard and soft dentine areas and increasingly arcuate grooves from anterior to posterior along the tooth row suggest that the mandibular movement pattern in *Nothrotheriops* is anterolingual, as in tree sloths and all other mammals except multituberculates studied to date (Hiimae, 1978). *Nothrotheriops* lacks the elongated caniniform teeth with their attendant restrictions, and shows more anteroposterior movement than does *Choloepus*. The direction and prominence of small striations and large grooves on each tooth indicate a stronger mediolateral component of motion in the power stroke in *Nothrotheriops* than in *Bradypus*.

The posterodorsal orientation of the ascending zygomatic process in *Nothrotheriops* had important functional consequences: it permitted a relatively vertical orientation of the lines of action of the anterior components of the *M. temporalis* and the *M. masseter superficialis* and these functions were correlated with the anteriorly positioned orbit and the position of the CMJ dorsal to the occlusal plane. As in *Bradypus*, *Nothrotheriops* lacks elongate caniniform teeth and has a CMJ above the occlusal plane and therefore can have a maximized mechanical advantage for the masticatory musculature. These effects are extreme in *Bradypus*, in which the ascending zygomatic process is more vertical, the *M. zygomaticomandibularis* and the *M. masseter profunda* relatively larger, and the face relatively shorter than in any other sloth. *Nothrotheriops* shows a similar trend in muscle arrangement, with a relatively large and vertically oriented *M. zygomaticomandibularis* and *M. masseter profunda*, but without the concomitant facial shortening. However, these muscles are not enlarged to the same relative degree as in *Bradypus*, perhaps because of other constraints related to the elongate nasal region for browsing and food ingestion in *Nothrotheriops*.

Dietary Requirements and Digestive Specializations in Sloths

Hansen (1978) determined from analysis of ground sloth dung in Rampart Cave, New Mexico, that composition of that sloth's diet resembled that of the desert mountain sheep, which presently inhabits the area, and therefore that the nutritional requirements of *Nothrotheriops* were probably similar to those of the sheep and other living large herbivores. Hansen also concluded from the size of the plant parts remaining undigested in dung balls that the sloths did not grind their foods to a fine particle size for digestion but rather "crunched and munched" it, swallowing large pieces. This is also true of the tree sloths *Bradypus* and *Choloepus* (Montgomery and Sunquist, 1975). The tree sloths are among the smallest folivores (Parra, 1973, 1978) and may be able to subsist on their low protein, high cellulose fiber diet partially

because of digestive specializations, but also because they maintain a low metabolic rate relative to their size, and thus have reduced energy demands per unit body weight (Almeida and Fialho, 1924; Britton, 1941; McNab, 1978). Such specializations could either allow sloths to have a minimized food intake, or to ingest lower quality foods. The tree sloths probably do both, and also have an unusually large gut capacity for their size (Britton, 1941) and a very long retention time for food in the gastrointestinal tract (Bauchop, 1978; Denis et al., 1967; Goffart, 1971; Jeuniaux, 1962; Moir, 1968; Parra, 1978). A bacterial flora is present in the stomach, and fermentation of the ingesta occurs there. It is reasonable to assume that ground sloths also had a low metabolic rate and that food was ingested in large quantities and remained for considerable time in the gut. Janis (1976) suggests that large body size permitted ruminant artiodactyls and perissodactyls to subsist on a high fiber diet because maintenance requirements per unit body weight decrease as body weight increases. In addition, ground sloth body shape suggests that these animals had room for an unusually capacious gastrointestinal tract, which would have permitted them to retain a (relatively) larger than usual amount of food for long periods of time. In combination, these factors would have made larger body size an advantage to ground sloths in general. These considerations, which correlate an increased foregut fermentation capacity with large body size agree with the trend toward increased body size shown throughout the fossil history of all ground sloth lineages, including that of the *nothrotheres*.

The existence of a foregut fermentation site in ground sloths is also supported by the presence of reduced or simplified molariform teeth with discontinuous shearing surfaces as in early and some modern ruminants (Janis, 1976). Although a lengthy dental grinding and crushing mill was apparently unimportant in food processing in ground sloths (perhaps because of the large gut capacity), extreme shortening of the face, as seen in *Bradypus* would have increased the difficulty of housing the long tongue typical of most xenarthrans and other herbivores. *Bradypus* has retained a large mobile tongue which is used extensively to ingest leafy materials in lieu of hand to mouth feeding, by having a uniquely modified hyoid apparatus located unusually far posteriorly relative to the position of the mandible (Naples, 1986). *Bradypus* has room for this arrangement because the long neck contains nine rather than seven cervical vertebrae. The more typical mammalian pattern of seven cervical vertebrae obtains in *Nothrotheriops*, making an arrangement similar to that of *Bradypus* less likely. For *Nothrotheriops*, as for many other long-tongued mammals, a relatively elongate face and flexible upper lip facilitates housing and using a tongue long enough to curl around and strip leaves and other plant parts from stems. A long tongue, flexible upper lip, and a mandibular premental spout would have been especially useful for food ingestion because the masticatory muscle arrangement may have precluded a gape wider than 25 degrees in *Nothrotheriops*. In addition, ground sloths probably used their forelimbs to reach for food as do tree sloths, but they probably could not manipulate small items with fine control, a problem

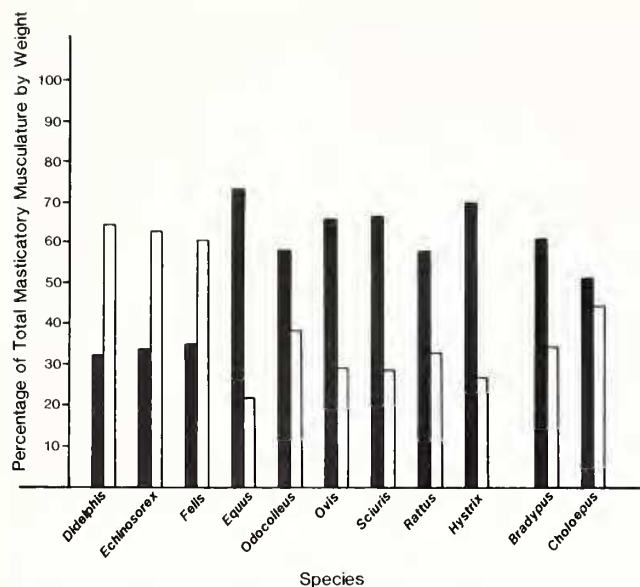


Figure 9. Percentages that the masseter-ptyergoid (solid bars) and temporalis complex (open bars) contribute to the total masticatory muscle mass in some carnivorous, insectivorous, and herbivorous mammals and the folivorous tree sloths. Data for all species except *Bradypus* and *Choloepus* were calculated from the masticatory muscle weights presented in Turnbull (1970).

shared with the much smaller tree sloths. Therefore, lips, tongue, and predental spout probably provided the most discrimination during food ingestion, and permitted sloths to be selective browsers, as Hansen's (1978) analysis suggests that they were.

Masticatory Muscle Structure and Function

Nothrotheriops resembles the tree sloths in masticatory muscle arrangement with muscle scars indicating similar muscle subdivision. Differences in relative muscle size and proportion exist, however, reflecting differences in cranial osteology among the groups. The following cranial characters were assigned polarities in *Nothrotheriops* determined by comparison with similar characters in tree sloths where polarities were determined and justified in Naples (1982, 1985a).

The masseter-ptyergoid complex. These muscles are comparably complex in all sloths, with similar relationships between origins and insertions among groups although the lines of action differ in direction. The *M. masseter superficialis* in *Bradypus* shows the most vertical, *Choloepus* intermediate, and *Nothrotheriops* the most anteroposteriorly directed line of action.

The *M. masseter profunda* differs greatly in size and direction between the tree sloths, being small and oriented posterodorsally (as in most mammals) in *Choloepus*, but greatly expanded and reoriented anterodorsally in *Bradypus*. In *Nothrotheriops* the muscle orientation resembles that of *Choloepus*, but because it originates upon an expanded posterodorsal zygomatic arch process it has become relatively

much larger and therefore could contribute a greater percentage of the force for jaw elevation and retraction than in *Choloepus*.

The pterygoid musculature in sloths is divided as in other mammals, although the direction of the line of action differs. The lateral pterygoid in *Choloepus* pulls anterodorsally as in other mammals, while in *Bradypus* the muscle pulls anteroventrally. The unusual muscle orientation in *Bradypus* obtains because the lateral pterygoid origin was carried ventrally with the ventral elongation of the pterygoid flanges (Naples, 1982, 1985a). The elongate pterygoid flange is one of a complex of characters associated with the elevated CMJ in *Bradypus*. In *Nothrotheriops* elongate pterygoid flanges also occur, the CMJ is elevated, and the muscle origin has been carried ventrally, resulting in an orientation similar to, but less extreme than, that seen in *Bradypus*. In addition to the typical medial and protrusive pull the *M. pterygoideus lateralis* exerts on the condyle in *Bradypus*, the reorientation of the muscle has introduced a downward component of force. The mandibular condyle in *Bradypus* is held medially against a bony projection during opening by this downward force. A bony stop is also present in *Nothrotheriops* and probably functioned with the *M. pterygoideus lateralis* as in *Bradypus*.

All three sloths have an *M. pterygoideus medius* similar in general orientation and probable action. The muscles differ in relative size, however, being smallest in *Choloepus*, somewhat larger in *Nothrotheriops* and largest in *Bradypus*. Again, these relative muscle sizes correlate with CMJ height above the cheek tooth row (zero in *Choloepus*, moderately elevated in *Nothrotheriops*, and strongly elevated in *Bradypus*).

The temporalis complex. In sloths the temporalis musculature is a smaller percentage of the masticatory muscle mass than in carnivores, and this muscle mass is equal to or greater in relative mass than in typical herbivores (Turnbull, 1970; Fig. 9). In tree sloths *M. temporalis* is incompletely divided into superficial and deep portions; no attempt to distinguish these portions was made in *Nothrotheriops*. The *M. temporalis* in *Bradypus* is relatively large in lateral view, because of the extremely short face in this sloth (Naples, 1985a), but is only 30 percent of masticatory muscle weight while that of *Choloepus* is somewhat more at 34 percent. Muscle weights, and therefore relative percentages of masticatory muscle mass are unavailable for *Nothrotheriops*, but muscle scars indicate that this muscle was similar to or slightly smaller than that of *Choloepus*. In *Nothrotheriops*, *M. temporalis* contributed less to the masticatory mass than its extensive area of origin would suggest because even in uncrushed specimens the temporal fossa was narrow and no sagittal crest was present. Therefore, in this sloth, *M. temporalis* was probably thin.

The *M. zygomaticomandibularis* differs dramatically in size but not orientation between the tree sloths. In *Choloepus* it is thin with fibers fanning anteroposteriorly to attach medially on the zygomatic arch. In *Bradypus* the muscle size is increased dramatically as allowed by the vertically expanded ascending zygomatic process (Naples, 1985a). The ascending zygomatic process in *Nothrotheriops* is expanded less and therefore the *M. zygomaticomandibularis* is intermediate in relative size between those of the two tree sloths.

In summary, *Bradypus* and *Choloepus* differ in relative masticatory muscle size. In *Choloepus* the masseter-pterygoid complex is only slightly dominant (Fig. 9) over the temporalis muscle group; this differs from other mammals so far studied. In contrast, *Bradypus* falls within the group defined as herbivores. Although the relative weight of muscle groups can only be estimated, *Nothrotheriops* can be predicted to fall between *Bradypus* and *Choloepus*. This is logical because among the herbivores the muscle mass values in *Bradypus* are most similar to *Odocoileus*, a browsing form (Turnbull, 1970; Fig. 9). It is also significant that *Ovis*, a genus that survived in the environment where *Nothrotheriops* became extinct, is a grazer, more similar to *Equus*, the most specialized of the forms discussed in detail by Janis (1976) and Turnbull (1970). While *Nothrotheriops* could subsist on the diet available these data suggest that slow-moving ground sloths with a low metabolic rate were not as efficient at selection, ingestion, and processing of the available foodstuffs as desert sheep. It is therefore possible that the sloths fared poorly in competition with the sheep for limited resources, even though they were probably equally able to subsist on the local flora.

Relationships of the Nothrotheres

It has been suggested (Winge, 1941; Patterson and Pascual, 1972; McKenna, 1975; Engelmann, 1985; Webb, 1985; Naples 1982, 1985a) that the tree sloths should not be united in the Bradypodidae, but allied to separate ground sloth lineages. These authors agree that *Choloepus* should be placed among the Megalonychidae and *Bradypus* among the Megatheriidae. The present cranial analysis contributes data supporting the derivation of *Bradypus* from the megatheriid lineage, as is *Nothrotheriops*, while *Choloepus* is not closely related to this group. Although *Bradypus* and *Nothrotheriops* differ dramatically in size and locomotor habits, they share derived cranial characters with other members of the Megatheriidae, not found in *Choloepus*, other members of the Megalonychidae, or the Mylodontidae. These characters include: (1) loss of elongate caniniform teeth, (2) a large antero-posterior component of movement during mandibular closing associated with (3) an elevated CMJ, (4) ventrally elongated pterygoid flanges which carry the lateral pterygoid muscle origin ventrally, causing (5) drastic reorientation of the line of action of this muscle, (6) an ascending process on the zygomatic arch which allows (7) expansion of the deep masseter and zygomaticomandibularis muscles, (8) a simple oval-shaped mandibular condyle with long axis directed anteroposteriorly, (9) an anteroposteriorly elongated and unrestricted glenoid fossa that limits the medial displacement of the mandibular condyle, and (10) a similar relationship between the proportions of the muscles of the masseter-pterygoid and temporalis complex. Although this study is not of broad enough scope to relate *Choloepus* and the megalonychids or to align *Bradypus* and *Nothrotheriops* within the Megatheriidae, it establishes some structural and functional similarities among these groups which can be used as criteria for making systematic decisions based upon derived char-

acters. Knowledge of such characters should improve the chances of refining sloth relationships in the future.

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